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AN EVOLUTIONARY AND GEOGRAPHICAL OVERVIEW OF REPAGULA (ABORTIVE EGGS) IN THE ASCALAPHIDAE (NEUROPTERA)

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Abstract.—Eggs and repagula (abortive eggs) were examined in seven previously unstudied species of Ascalaphidae from both the Old and New World. In those forms that possess repagula, the ratio of egg length to repagulum length is shown to be an unreliable taxonomic character. The absence of repagula in all Old World split-eyed taxa so far examined is interpreted as a secondary loss in a monophyletic assemblage of owlflies derived from a rather primitive New World ancestor—a view substantiated by ovariole number and larval morphology. New World ascalaphids show progressive specialization in repagulum form and function from primitive entire-eyed genera like *Byas* and *Ascaloptynx* to derived split-eyed ones like *Ululodes* and *Cordulecerus.* Entire-eyed *Episperches* and split-eyed *Colobopterus* are judged transitional.

The Reverend L. Guilding (1827) coined the term "repagula" to describe the small, glossy, rod-shaped bodies that accompany the egg masses of certain split-eyed (ascalaphine) Ascalaphidae. These structures encircle each egg-bearing twig like a fence immediately below the fertile eggs: appropriately, the meaning of the Latin word *repagulum* is "little barrier." Henry (1972) verified the protective function of repagula against insect predators in *Ululodes mexicana* (McLachlan), which possesses eggs with very thin shells.

McClendon (1902) demonstrated that the repagula of *Ululodes* are in fact highly modified abortive eggs that develop in their own specialized ovarioles. More recently, New (1971) determined that abortive eggs are also characteristic of entire-eyed (neuroptyngine) Ascalaphidae, but that in these latter forms the structural differences between infertile and fertile eggs are slight. Henry (1972) showed that the abortive eggs of at least one neuroptyngine, *Ascaloptynx furciger* (McLachlan), serve as food for the newly enclosed larvae and perhaps provide them with the nourishment necessary for group defense against ants and other predators. Repagula of *Ascaloptynx*, then, are not true barriers and in fact lack the repellant fluid coating found on the repagula of *Ululodes* (Henry, 1972). Other studies have shown that in the neuroptyngine genus *Byas* Rambur the repagula share a common morphology with those of *Ascaloptynx*, while ascalaphines such as *Cordulecerus* Rambur, *Colobopterus* Rambur, and *Ascalorphne* Banks, possess repagula very similar to those of *Ululodes* (New, 1971; Henry, In Press). Repagula of intermediate form are characteristic of the specialized neuroptyngine genus *Episperches* Gerstaecker (New, 1971).

All ascalaphid genera mentioned above are restricted to the New World, but both the split-eyed and entire-eyed owlfly subfamilies have nearly world wide distributions. Early European insect anatomists—e.g., Brauer (1854) and Dufour (1860)—neither discuss nor figure anything resembling modified ovarioles in *Ascalaphus macaronius* Scopoli or *A. meridionalis* Charpentier. Other works that describe the egg masses of Old World Ascalaphidae make no mention of egg attendants (Westwood, 1888; Ghosh, 1913; Fraser, 1957). The implication is that none of the Old World owlflies oviposits repagula, while members of both subfamilies in the other hemisphere do so.

The present study introduces data on egg and repagula production in several other species of Ascalaphidae, including *Helicomitus dicax* (McLachlan), *H. festivus* (McLachlan), *Suphalomitus malayanus javanensis* Weele, *Hybris subjacens* (Walker), *Ascalaphus libelluloides* Schäffer, *Cordulecerus alopecinus* Burmeister, and *Colobopterus* sp. near *trivialis* and *consors* Gerstaecker. In each case, the presence or absence of repagula is noted, based either upon dissection of gravid females or upon study of field-collected egg masses. Numbers of normal and modified ovarioles per ovary are given whenever possible, and measurements of the proportions of eggs and attendants are tabulated. These data are compared with those of previous authors. The possible biogeographical and phylogenetic significance of the results is then discussed.

Methods and Materials

Adult ascalaphids suitable for dissection were preserved in 75% EtOH and examined under a WILD™ M5 stereoscopic dissecting microscope fitted with 10× eyepieces. Eggs and other structures were figured and measured by means of a *camera lucida* attachment for this microscope.

Material for the study came from several sources. The adult specimens from Shanghai, Madagascar, Java, and Paraguay were part of an extensive alcoholic collection of poorly labeled insects deposited in the Museum of Comparative Zoology (Harvard University) by the late G. C. Crampton. Egg masses of *Ascalaphus libelluloides* were collected by my wife and myself in the vicinity of Penne, Tarn et Garonne, France, during the last half of July, 1974. Eggs and repagula of the Panamanian ascalaphid *Colobopterus* sp. A were obtained from a captive female by R. E. Silberglied and A. Aiello on 26 May 1976, on Barro Colorado Island, Canal Zone, Panama. The identities of all adults were determined from Weele's (1908) monograph, while larvae of *Ascalaphus libelluloides* were identified from the keys of Rousset (1973). Comparative data on *Ululodes mexicana* and *Ascaloptynx furciger* were drawn from material assembled for an earlier study (Henry, 1972).

Results

Results are summarized chiefly in Table 1. The Ascalaphinae species studied belong to four of the seven accepted tribes of the subfamily: Suhpalacsini (*Helicomitus* and *Suphalomitus*), Hybrisini (*Hybris*), Ascalaphini (*Ascalaphus*), and Ululodini (*Cordulecerus* and *Colobopterus*). The Old World tribes Proctarrelabrini, Acmonotini and Encyoposini are not represented. Females of Old World taxa all have ten egg producing ovarioles per ovary; no specimens contained abortive eggs. On the other hand, the two New World species possess repagula within specialized ovarioles and display marked differences between the proportions of the fertile eggs and those of the egg attendants. Eggs of *Cordulecerus alopecinus* were by far the largest in the ascalaphines studied, while the most spherical (broadest) were found in *Ascalaphus libelluloides*. Repagula of *Colobopterus* sp. A were proportionately much longer and thinner than those of *Cordulecerus*, being only fractionally shorter than the eggs themselves (ratio of egg length/repagulum length = 1.10). Egg size varied markedly among individuals in both species of *Helicomitus* and in *Hybris subjacens* but did not appear to be closely correlated with maternal dimensions except in *H. dicax* (Table 2).

It may be argued that the sizes of eggs and repagula obtained from dissected females are not comparable to those of the same structures when oviposited. To test this, eggs and attendants obtained by dissection were compared with those attached to twigs in *Ululodes mexicana*, an ululodine ascalaphine species from southern North America. The results (Table 3) indicate that sizes are insignificantly different in each of the two classes of data and that the pooling of data for both unlaid and oviposited eggs or repagula of Ascalaphidae is probably valid.

Table 4 compares the ratio of egg length to repagulum length in masses obtained from several different individuals of both *Cordulecerus alopecinus* and *Ululodes mexicana*, in order to test New's (1971) hypothesis that this ratio is a reliable taxonomic character separating the egg masses of closely related species of New World Ascalaphinae. The ratio was found to vary widely in *U. mexicana*, ranging from 1.65–2.19 in the five masses reliably measured. The ratios obtained from four *Cordulecerus alopecinus* dissections ranged from 1.73–1.99. The ovariolar number is seven in *Ululodes mexicana* and eight in *Cordulecerus alopecinus*; both species possess four additional repagula-bearing ovarioles in each ovary.

Discussion

The results strengthen the hypothesis that repagula production is limited to Ascalaphidae of the New World. Previously, it was suspected only that members of the Old World genus *Ascalaphus* lacked abortive eggs

Table 1. Comparisons of egg and repagulum dimensions and of ovariole numbers for eight species of Ascalaphidae. Measurements of eggs and repagula were obtained both by dissection of gravid females (preserved in alcohol) and by examination of oviposited masses.

	Taxon	Collecting site	Structure	No. of diff. indivs. or egg masses	No. of ovarioles	Sample size	Mean length ± SD (mm)	Mean breadth ± SD (mm)
	Neuroptynginae							
New World	*Ascaloptynx furciger* (McLachlan)	N. America (Arizona)	Eggs	5 masses	—	19	2.21 ± .120	1.26 ± .046
			Repagula	3 masses	—	17	1.33 ± .101	0.68 ± .084
	Ascalaphinae							
Old World	*Helicomitus dicax* (McLachlan)	S.E. Asia (Shanghai)	Eggs	3 ♀♀	10	18	1.57 ± .250	0.90 ± .180
			No Repagula					
	Helicomitus festivus (McLachlan)	Madagascar	Eggs	3 ♀♀	10	17	1.36 ± .270	0.76 ± .110
			No Repagula					
	Suphalomitus malayanus javanensis Weele	S.E. Asia (Java)	Eggs	1 ♀	—	6	1.70 ± .156	0.99 ± .115
			No Repagula					
	Hybris subjacens (Walker)	S.E. Asia (Java)	Eggs	2 ♀♀	10	17	1.41 ± .194	0.80 ± .074
			No Repagula					
	Ascalaphus libelluloides Schäffer	Europe (S. France)	Eggs	6 masses	—	29	1.61 ± .085	1.19 ± .051
			No Repagula					
New World	*Corduleceras alopecinus* Burmeister	Paraguay	Eggs	4 ♀♀	8	26	2.28 ± .078	1.21 ± .073
			Repagula	4 ♀♀	4	38	1.23 ± .073	0.28 ± .017
	Colobopterus sp. A. near *trivialis* & *consors* Gerstaecker	Panama	Eggs	1 mass	—	10	1.52 ± .049	0.77 ± .015
			Repagula	1 mass	—	2	1.35 – 1.40	0.21 – 0.23

Table 2. Major morphological measurements of individual ascalaphid adults compared with the dimensions of eggs obtained from the same individuals by dissection. Adult measurements include the lengths of body, forewing, and antenna and the width of the head across the eyes.

	Adult measurements (mm)				Egg measurements (mm)		
	Body L	Forewing L	Antennal L	Head W	Mean length ± SD	Mean breadth ± SD	*N*
Helicomitus dicax							
A	22.0	27.0	18.5	5.5	1.48 ± .058	0.80 ± .036	7
AA	22.0	26.5	18.0	5.3	1.28 ± .027	0.73 ± .045	5
A-3	23.0	29.0	19.0	6.0	1.90 ± .043	1.14 ± .023	6
Helicomitus festivus							
B	27.0	28.0	23.0	5.7	1.25 – 1.30	0.80	2
BB	25.0	27.0	22.0	5.5	1.63 ± .075	0.85 ± .044	8
B-3	27.0	29.0	20.0	5.7	1.09 ± .075	0.65 ± .024	7
Hybris subjacens							
D	28.0	35.0	30.5	5.6	1.29 ± .141	0.75 ± .045	10
DD	29.0	33.0	30.0	5.6	1.59 ± .073	0.87 ± .033	7

and associated modified ovarioles. The present work extends this suspicion to representatives of the ascalaphine tribes Suhpalacsini and Hybrisini and confirms the absence of repagula in the major constituent and nominate genus of Ascalaphini. Unfortunately, nothing is known of repagula formation in Old World Neuroptynginae; however, Fraser (1922) does not mention attendants accompanying the fertile eggs of *Balanopteryx umbraticus* Fraser in Madagascar.

Repagula production in New World ascalaphine owlflies is best in-

Table 3. Dimensions of eggs and repagula obtained from five dissected females of *Ululodes mexicana* compared with those obtained from three oviposited egg masses of the same species.

	Structure	No. of diff. indivs. or egg masses	Sample size	Mean length ± SD (mm)	Mean breadth ± SD (mm)
From	Eggs	5 females	40	1.89 ± .159	0.94 ± .083
Dissected Females	Repagula	5 females	50	0.99 ± .176	0.22 ± .028
From Oviposited	Eggs	3 masses	14	1.90 ± .099	1.06 ± .049
Egg Massess	Repagula[A]	2 masses	15	0.93 ± .084	0.23 ± .024

[A] From masses preserved in alcohol; dried egg masses possess eggs of normal size but withered repagula.

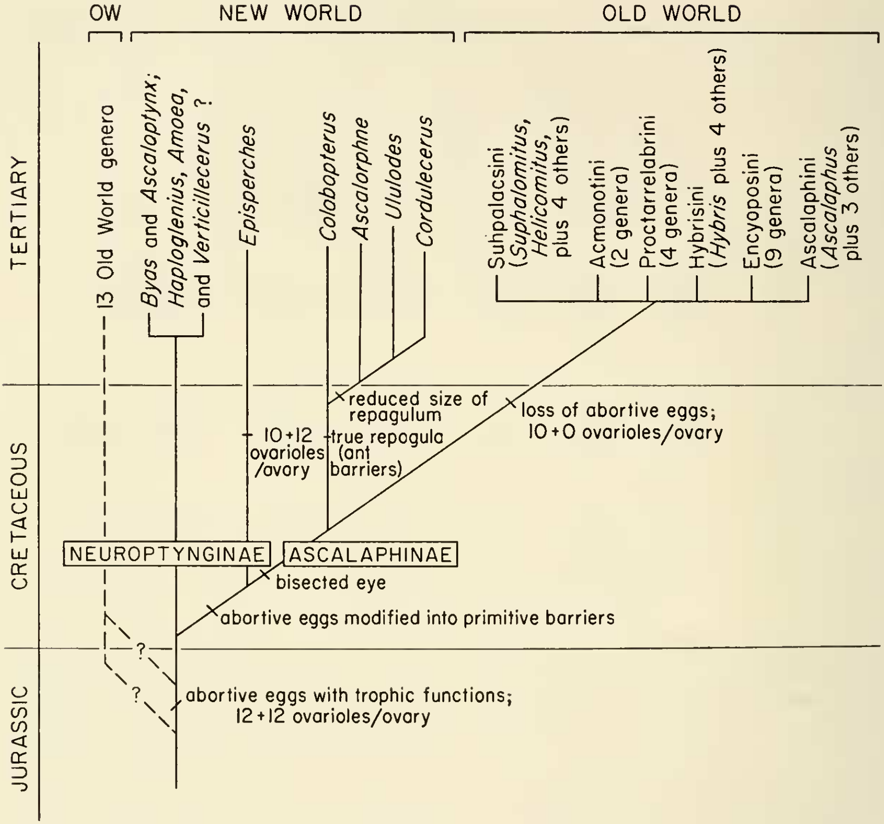

Fig. 1. Phylogeny of Ascalaphidae based upon structure of adult eyes, ovarioles, and repagula.

terpreted as a specialization within a monophyletic assemblage of insects (Fig. 1). All New World ascalaphids of the split-eyed subfamily are closely similar to one another in wing venation, abdominal terminalia, and antennal morphology and have been placed—in my view correctly—in a single tribe, the Ululodini (Weele, 1908). Similar types of fluid-covered repagula are found in representatives from every genus of the tribe. The effectiveness of the repagula against potential predators remains to be tested in taxa other than *Ululodes*.

New (1971) speculated that the repagulum of Ululodini is derived from one like that in the Neuroptynginae; the unavoidable implication from his paper is that the transition from a "simple" abortive egg like that of *Byas* to the specialized "rods" or "dumb-bells" of Ululodini occurred through some more specialized neuroptyngine genus (like *Episperches*) possessing repagula of intermediate morphology. Such views receive additional support from data given in Table 1 and in two previous papers (Henry, 1972 and In Press). However, the absence of any sort of abortive eggs in Old World ascalaphids is difficult to reconcile with a scheme that derives split-eyed owlflies from entire-eyed ancestors. Presumably, abortive egg production is a shared specialization of all Ascalaphidae, with further modification of abortive eggs into true repagula (predator barriers) occurring within certain Neuroptynginae that then gave rise to Ascalaphinae; this is the hypothesis borne out by data on New World forms. If this is true, one would expect to find egg attendants in some Old World taxa regardless of the evolutionary relationships among family members. For example, generalized Old World members of both subfamilies should possess unspecialized abortive eggs if one assumes that New World forms evolved from Old World ancestors that had already differentiated into two types with different eye morphology. Alternatively, the Old World ascalaphines, neuroptyngines, or both, might be derived from New World ancestors; in these cases, it is likely that split-eyed Old World taxa would retain and perfect some sort of specialized repagulum similar to that of Ululodini. Loss of repagula in derived taxa is possible, but the greater adaptive value to the eggs of attendants once the latter assume a protective function renders this hypothesis unattractive, as well. Unfortunately, too little is known of other aspects of ascalaphid morphology and biology to clarify the phylogenetic puzzle. However, larval morphology (Henry, 1976) and the orientation of eggs in naturally-occurring egg masses (Henry, 1972) suggest that New World Ascalaphinae are highly specialized in comparison with their Old World relatives; among other implications, this makes the secondary loss of egg attendants in the latter group seem even less likely.

If one assumes that repagula have not been lost secondarily, one must conclude that monophyly either of split eyes or of repagula production is an incorrect interpretation of ascalaphid evolution. Either aspect of this conclusion is difficult to accept. On the one hand, comparative morphology of the sulcate eyes of Old and New World Ascalaphinae indicates that the bisection is almost certainly homologous in representatives from the two hemispheres (Fig. 2). On the other hand, as far as is known, production of abortive or trophic eggs from modified ovarioles is unique to Ascalaphidae within the Neuroptera and very rare in other insect orders; the convergent evolution of such an apomorphy separately in Ascalaphinae and Neuroptynginae of the Western Hemisphere seems unlikely. What appears to be progressive increase in specialization of repagula from entire-eyed to split-eyed taxa in the New World is further evidence against convergent evolution of egg attendants in the two subfamilies; one may even interpret the *Colobopterus* repagulum as intermediate between that of *Episperches* and those of higher Ululodini (Fig. 3). Therefore, I feel

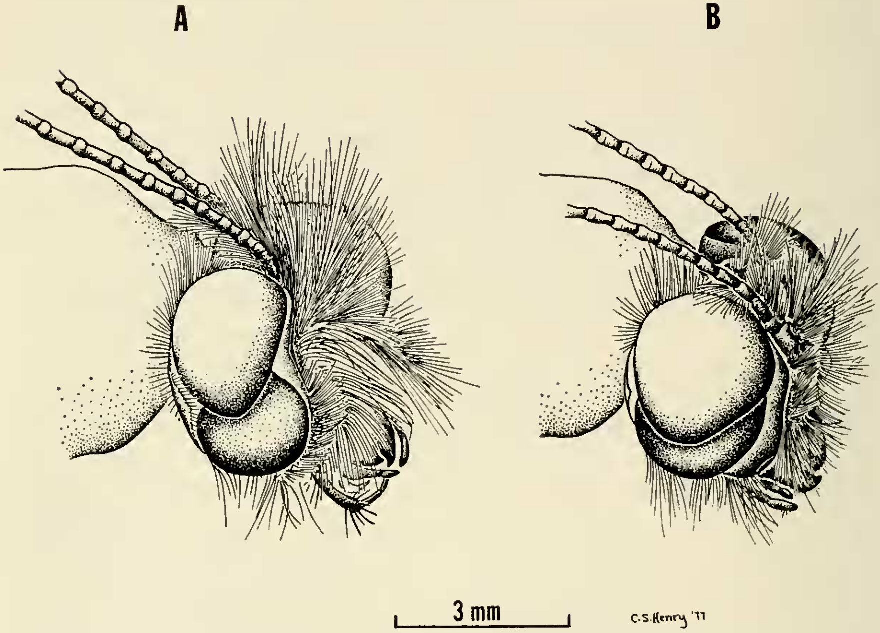

Fig. 2. Fronto-lateral view of the head of New World (A) and Old World (B) ascalaphine owlflies, showing bisected eyes. A = *Ululodes mexicana* and B = *Helicomitus dicax*.

that it is better at the present time reluctantly to postulate loss of repagula in Old World Ascalaphinae and to assume that all owlfly taxa in all geographical areas originated from New World neuroptyngine ancestors possessing primitive abortive eggs; bisection of the eye must also have developed first in the Western Hemisphere, with early colonization of the Old World by a primitive ascalaphine stock (Fig. 1). The position of African and Asian Neuroptynginae is uncertain in such a scheme since their eggs are so poorly known.

The presently uncertain systematic position of *Colobopterus* is rendered even more problematical by repagular morphology. Although it is widely accepted that *Ululodes quadrimaculata* (Say) is the female of *Colobopterus excisus* Hagen in North America, the *Colobopterus* sp. A near *trivialis* and *consors* discussed here is markedly divergent from any known species of *Ululodes* in the form and size of its egg attendants. Additionally, the larval morphology of another Panamanian species of the genus, *Colobopterus* sp. B near *mulleri* Weele, is totally unlike that of any known *Ululodes* (unpublished data). Consequently, it is probably valid to exclude some species of *Colobopterus* from *Ululodes*; in fact, the magnitude of repagular

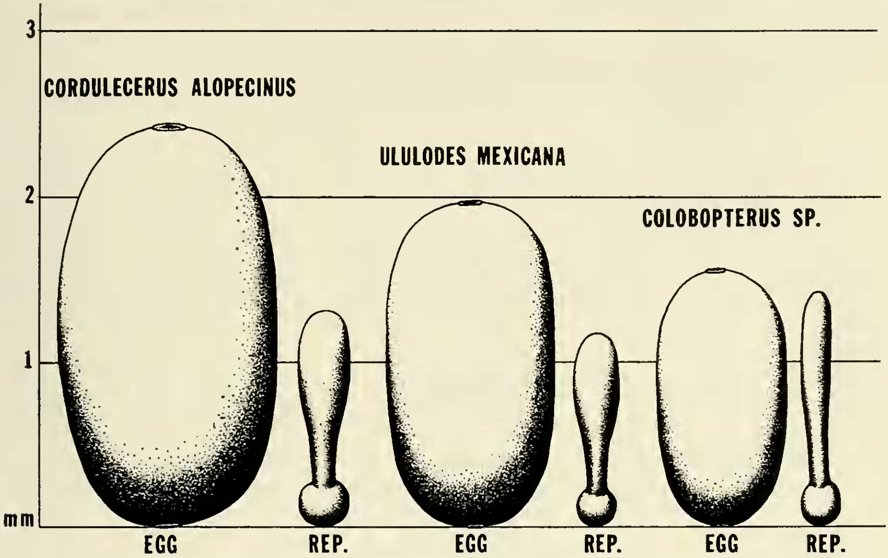

Fig. 3. The eggs and repagula of three New World owlflies of the tribe Ululodini, drawn to the same scale. REP. = repagulum.

and larval differences just mentioned suggests that some *Colobopterus* species are less closely related to *Ululodes* than is *Cordulecerus*, which possesses a *Ululodes*-like repagulum (Fig. 3).

Comparative measurements of eggs and repagula (Table 4) do not support New's (1971) contention that "the ratio of repagula [*sic*] length:egg length affords an index for separation of the egg masses of closely related species." In neither *U. mexicana* nor *Cordulecerus alopecinus* is such a ratio constant. At one extreme, the ratios for *Ululodes mexicana* are found to overlap extensively with those calculated from New's data for both *U. macleayana* near *limbata* Burmeister and *U. aurifera* McLachlan. At the other extreme, egg/repagulum ratios for New's *Cordulecerus alopecinus* are significantly different from my own measurements on the same species (1.37 vs. 1.88 ± .11, $N = 4$). Unfortunately, New gives neither means nor standard deviations of his data and does not make clear how many different egg masses his sample sizes represent.

The phylogenetic significance of ovariole number in Ascalaphidae has not been assessed. Within the Neuroptera as a whole, primitive taxa seem to exhibit larger numbers of ovarioles. For example, alderflies (Megaloptera: Sialidae) have up to 100 egg tubes per ovary (Matsuzaki and Ando, 1977), while green lacewings (Planipennia: Chrysopidae) possess only 12–15 (Hwang and Bickley, 1961; Rousset, 1976). New (1971) reported

Table 4. Comparisons of egg and repagulum lengths and of ovariole numbers for nine dissected individuals of *Ululodes mexicana* and four of *Cordulecerus alopecinus*. The ratio of egg length to repagulum length is calculated for each insect.

	No. of ovarioles/ovary		Mean length ± SD (mm)		Ratio of egg length: repagulum length
	bearing eggs	bearing repagula	Eggs (*N*)	Repagula (*N*)	
Ululodes mexicana					
Skel.	–	–	1.95 ± .038 (5)	0.89 ± .053 (10)	2.19
DS-1	?	4	1.83 ± .087 (10)	1.04 ± .039 (7)	1.76
DS-2	?	4	1.70 ± .113 (9)	1.03 ± .063 (10)	1.65
DS-3	?	?	1.86 ± .095 (3)	0.72 ± .034 (13)	2.58
DS-4	7	4	immature		
DS-5	7	4	2.04 ± .073 (10)	1.17 ± .086 (11)	1.74
DS-6	7	4	2.02 ± .087 (8)	1.08 ± .036 (9)	1.87
DS-8	7	4	immature		
DS-9	7	4	immature		
Cordulecerus alopecinus					
E	–	–	2.29 ± .078 (8)	1.20 ± .032 (11)	1.99
EE	–	–	2.34 ± .046 (6)	1.24 ± .045 (8)	1.89
E-3	8	4	2.21 ± .047 (5)	1.16 ± .042 (9)	1.91
E-4	8	4	2.26 ± .083 (7)	1.31 ± .071 (10)	1.73

fairly high ovariole numbers of 22–24 in most of the owlflies he dissected, although repagula occupied twelve of the tubes. The neuroptyngine *Episperches arenosus* (Walker) showed a reduction from twelve to ten in the number of egg-producing ovarioles per side, while *Ululodes aurifera* of the Ascalaphinae exhibited only eight "fertile" and four "modified" tubes in each ovary. The present study confirms that these numbers need not be constant in a genus, since the ovary of *U. mexicana* has one less fertile ovariole than that of *aurifera* (Table 4)[1]. The discrepancy noted within *Cordulecerus alopecinus* between my own counts of ovarioles (8 + 4 per side) and those of New (12 + 12) indicates almost certainly that the two studies were not based on conspecific individuals. This might explain the differences obtained in egg/repagulum ratios, as well.

Old World ascalaphine forms examined here possess only ten ovarioles per ovary, as do members of the Eurasian genus *Ascalaphus* (Brauer, 1854; Dufour, 1860). Such a reduced ovariolar number is best interpreted as a specialization; the fact that it is shared by representatives of the tribes

Suhpalacsini, Hybrisini, and Ascalaphini from Europe, Asia and Africa strongly suggests close relationship among these taxa. The extant Old World Ascalaphinae, then, may indeed represent an adaptive radiation from the single primitive New World stock postulated earlier in the discussion. That this and all other evolutionary events within the Ascalaphidae took place after the separation of South America from Australia is strongly indicated by the total absence of Neuroptynginae from the latter continent; probably Africa and South America were in close proximity when owlflies with bisected eyes originated. Subsequent isolation of African Ascalaphinae by drifting of the continents in the Cretaceous produced the morphologically and behaviorally distinct Old World forms that we see today (Dietz and Holden, 1970). In the New World, repagula capable of repelling predators certainly arose subsequent to the establishment of a dominant ant fauna or "mosaic": at the earliest, within the Upper Cretaceous (Leston, 1973). This gives an independent approximate dating of certain later events of ascalaphid evolution synchronous with that derived from drift theory.

Acknowledgments

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Footnote

[1] An earlier study (Henry, 1972) reporting eight fertile egg tubes in *U. mexicana* is in error.